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REVIEW

Functional Ecology



Are ecophysiological adaptive traits decoupled from leaf economics traits in wetlands?

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Abstract

1. Wetland plants have developed a suite of traits, such as aerenchyma, radial oxygen loss and leaf gas films, to adapt to the wetland environment characterised by, for example, a low redox potential and a lack of electron acceptors. These ecophysiological traits are critical for the survival and physiological functioning of wetland plants. Most studies on these traits typically focus on a single trait and a single or few species at the time.
2. Next to these traits, traits of the leaf economics spectrum (LES) that reflect resource acquisition and allocation in plant species have also been frequently measured in wetlands. However, the performance of the LES has rarely been examined among wetland plants.
3. Both suites of traits are critical for—but affect different aspects of—wetland plant functioning and survival. The interactions between them, potentially causing synergies or trade-offs, reflect wetland plant strategies to simultaneously deal with stress tolerance and resource utilization, and have ramifications for the functioning of wetland ecosystems.
4. Based on a literature review and quantitative analysis of available data, we provide evidence suggesting that LES and ecophysiological traits may be decoupled (e.g., for root porosity and radial oxygen loss vs. leaf nitrogen) or coupled (e.g., for iron tolerance vs. specific leaf area) in wetlands, depending on the trait combination concerned. This rather complex relationship between wetland adaptive traits and LES traits indicates that there can be multiple mechanisms behind the strategies of wetland plants.
5. We further illustrate how adaptive and LES traits together contribute to wetland ecosystem functions, such as denitrification and methane emission. We highlight that both suites of traits should be considered simultaneously when applying trait-based methods to wetland ecology.

KEYWORDS

adaptation, ecophysiology, ecosystem functioning, leaf economics spectrum, plant adaptive strategy, trait-based method, wetland adaptive traits, wetland ecology

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1 | INTRODUCTION

Wetland ecosystems include a wide variety of fresh and saltwater habitats (e.g., marshes, peatlands, mangroves, rivers, lakes, intertidal mudflats and rice paddies) that are distinguished from terrestrial habitats by a different hydrological regime (Ramsar Convention Secretariat, 2013). This causes wetland ecosystems to have unique features in terms of oxygen availability, nutrient cycles, soil pH and redox potential. These deviating environmental conditions strongly affect the survival and functioning of wetland plants. In response, wetland plants have developed a suite of adaptive traits, including tolerance and escape traits, to waterlogging or inundation and other conditions characteristic of wetlands (DeLaune & Pezeshki, 2001; Jackson & Armstrong, 1999; Pezeshki & DeLaune, 2012). These traits are strongly related to wetland plant performance, sometimes even vital to their survival. Previous studies on these adaptive traits have commonly focused only on one or a few species at the individual level, which makes these adaptive traits hard to incorporate into trait-based wetland ecology. In contrast, leaf economics spectrum (LES) traits such as leaf nitrogen (leaf N), leaf phosphorus (leaf P), specific leaf area (SLA) and photosynthetic rate (A_{mass} or A_{area}) have received more attention, but do not include those traits that are considered vital to the survival of plants under wetland conditions in ecophysiological studies (van Bodegom, de Kanter, Bakker, & Aerts, 2005; Visser, Colmer, Blom, & Voeselek, 2000; Voeselek & Bailey-Serres, 2015).

Moreover, the functional importance of most traits is context-specific (Bastrop-Spohr, Sand-Jensen, Nicolajsen, & Bruun, 2015; Shipley et al., 2016; Wright & Sutton-Grier, 2012). This context may well differ for wetland ecosystems compared to terrestrial ecosystems, because trait selection is strongly driven by environmental factors (van Bodegom et al., 2012; DeLaune & Pezeshki, 2001). A recent review paper (Moor et al., 2017) carefully reviewed both wetland adaptive traits and LES traits as well as their effect on ecosystem functioning, and the authors suggested not to simply employ the LES/plant economics spectrum (PES) to understand wetland ecosystems, since they vary widely in site conditions (bogs, peatland, marsh etc.). The study called for the inclusion of LES/PES and adaptive traits to get a better understanding of wetland ecology. To move towards this goal, we need to understand how these two groups of traits, if taken as the two major trait axes, position in relation to each other. In other words, it is important to disentangle the different roles that wetland adaptive traits and LES traits play in plant survival and resource utilization, respectively, their relationships being orthogonal (reflecting a decoupling) or coordinated (reflecting coupling through synergies or trade-offs), and the consequent effects on ecosystem functioning.

The adaptive response and the physiological mechanisms of adaptive strategies to wetland conditions have been carefully examined in ecophysiological studies, which have shown adaptation in traits in relation to root morphology and plant physiology (Colmer, 2003a; Laan, Berrevoets, Lythe, Armstrong, & Blom, 1989; van Bodegom et al., 2005). For instance, plants can adapt

to cope with the oxygen deficiency associated with waterlogging/flooding by developing adventitious roots or aerenchyma in shoots or roots (Blom et al., 1994; Justin & Armstrong, 1987; Wright et al., 2017), or enhancing root porosity (Garthwaite, von Bothmer, & Colmer, 2003; Justin & Armstrong, 1987). Likewise, radial oxygen loss (ROL) protects plant roots from anaerobic stress (Lemoine, Mermillod-Blondin, Barrat-Segretain, Massé, & Malet, 2012), whereas barriers to ROL in basal zones enhance longitudinal oxygen diffusion towards the apex (Colmer, 2003a). Phytohormones such as ethylene, gibberellin and abscisic acid also play important roles in changing cellular and organ structure that alleviate the oxygen deficiency (Bailey-Serres & Voeselek, 2008; Vartapetian & Jackson, 1997). Most of these primarily ecophysiological studies on wetland plants, though, are limited to an experiment-based assessment of one individual trait for a few species at a time. Unfortunately, it is rather difficult to scale up results from such detailed studies to the impacts of different plants and communities on wetland ecosystem functioning. Therefore, we need to integrate these ecophysiological traits into a more general ecological framework (Figure 1a).

There is some circumstantial evidence that wetland adaptive traits may be orthogonal to (i.e., independent of or decoupled from) LES/PES: wetland adaptive traits are the premise of plant existence in wetlands since they are vital to the survival of plants under hazardous anaerobic conditions. Based on that premise, one may expect trait selection processes in wetlands to be strong. At the same time, while LES traits are principally constrained by nutrient availability (Maire et al., 2015), wetland habitats span a wide fertility gradient from very infertile bogs to very fertile floodplains/marshes at a global scale. This provides the conditions to allow for a full range of leaf N if wetland adaptive traits are orthogonal to LES/PES (Figure 1b). However, if trade-offs between the two axes predominate, one would expect only a subset of LES/PES would remain available for wetlands (Figure 1c). The wide variety of growth strategies in wetlands, from conservative strategies associated with, for example, bogs to acquisitive strategies in highly productive systems such as reed lands, suggests that wetland plants can sufficiently develop adaptive traits to cope with multiple and varied wetland conditions. This pattern also suggests an orthogonal relationship between adaptive traits and LES/PES traits.

In this paper, we present an exploratory analysis to quantify the relationships between wetland adaptive traits and LES/PES traits. We hypothesize that adaptive traits are principally decoupled from LES/PES traits in wetlands, assuming that these adaptive traits are not costly to have. Consequently, we predict that we will see a wide range of LES/PES in wetland plants. Using published and unpublished data, we assess the relationship between wetland adaptive traits and LES/PES traits. Then, we illustrate how wetland adaptive traits and LES/PES traits together impact wetland ecosystem functioning.

While the lack of integration of wetland adaptive traits into more generic trait-based approaches has formed a barrier to the direct employment of trait-based methods to wetland ecosystems to date, we propose that a more comprehensive understanding of wetland

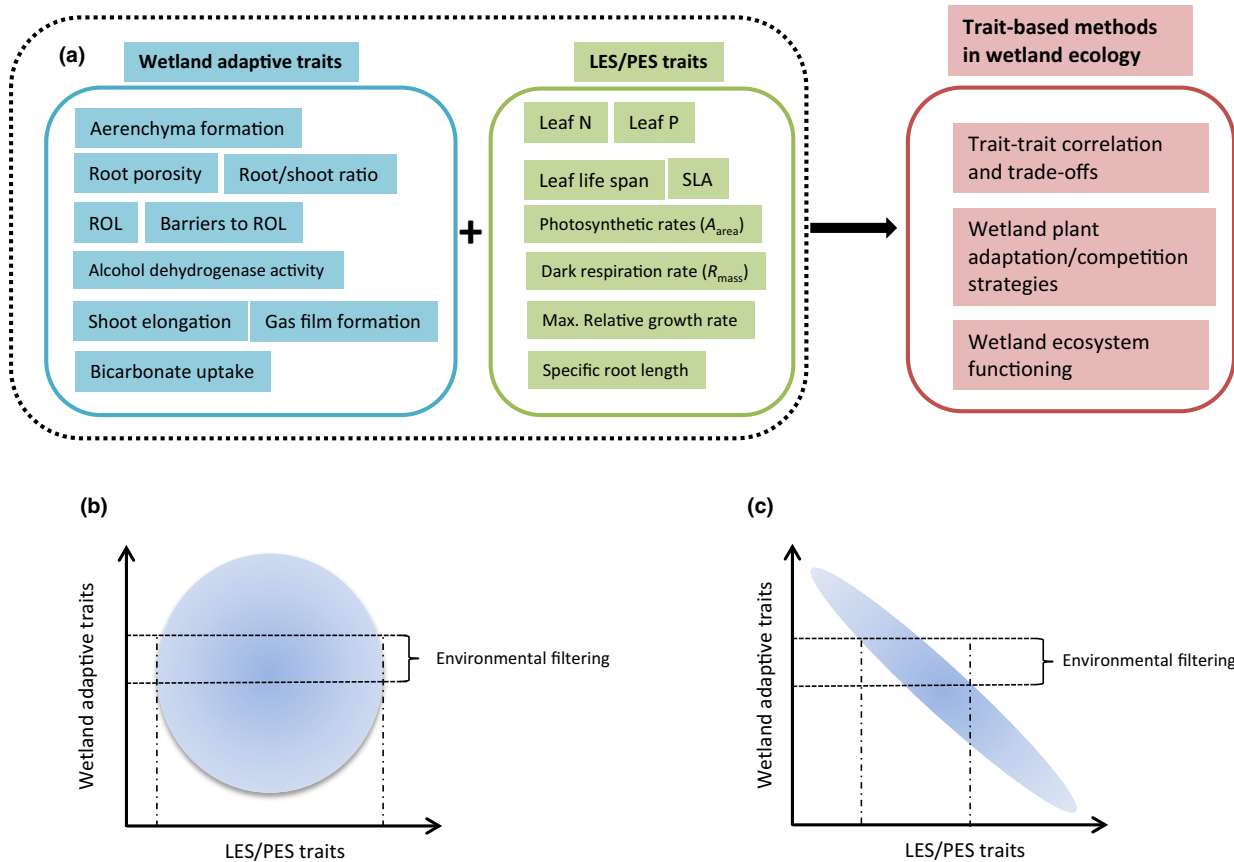


FIGURE 1 A summary of most commonly studied wetland adaptive traits and leaf economics spectrum (LES)/plant economics spectrum (PES) traits (a); the relationships between these two suites of traits determine wetland plant adaptive and competitive strategies, and wetland ecological functioning. If wetland adaptive traits are orthogonal to LES/PES, even if environmental filtering to a specific setting of the water regime selects a subset of adaptive traits, almost a full range of LES/PES trait values would still be visible among wetland species (b). If trade-offs are predominant, environmental filtering of wetland conditions selects a subset of adaptive traits, and consequently, only a corresponding subset of LES/PES remains (c)

ecology can be obtained through the quantification of the relationships between the two suites of traits. This will also allow us to make better-informed decisions with respect to one of the standard dilemmas in trait-based community ecology: the choice of measuring traits for ease of measurements and low cost versus functional/mechanistic importance (Lavorel & Garnier, 2002; Wright et al., 2010).

2 | LITERATURE REVIEW ON THE RELATIONSHIPS BETWEEN WETLAND ADAPTIVE TRAITS AND LES/PES TRAITS

Some trade-offs among wetland adaptive traits and nutrient uptake have been described. In general, wetland plants may experience more nutrient stress than other plants under similar conditions of nutrient availability, because some adaptation to oxygen or redox stress result in a reduced adaptation to nutrient stress (Silvertown, Araya, & Gowing, 2015). In turn, this is likely to negatively affect leaf nutrient contents, which are part of LES/PES. For instance, decreasing root respiration and increasing aerenchyma leave less energy and active root biomass, respectively, for the active uptake of nutrients

(van der Werf, Kooijman, Welschen, & Lambers, 1988). A root barrier that retards oxygen leakage may also reduce the efficiency of nutrient uptake (Colmer, 2003b), although studies suggest that symplastic aquaporin activity can prevent this effect (Rubinigg, Stulen, Elzenga, & Colmer, 2002). In some cases, cortical aerenchyma also inhibits nutrient transport (Hu, Henry, Brown, & Lynch, 2014). Another trade-off includes a decrease in phosphate availability in the presence of ROL by the oxidation of Fe^{2+} in the rhizosphere, inducing the precipitation of phosphate with iron. If these trade-offs are representative of the strategies of wetland plant species, then wetland plant species should occupy the lower ranges of the LES/PES.

In the case of SLA, such a relationship is rather complex as SLA may be seen as part of LES/PES and other plant strategy axes, such as the size axis (Wright et al., 2010), and it may also relate to wetland plant's adaptation to water stress. For example, community mean SLA increased with flooding, suggesting that SLA contributed to the plant's waterlogging tolerance (Violle et al., 2011). Also, Mommer, Wolters-Arts, Andersen, Visser, and Pedersen et al. (2007) found, across nine species, that the internal oxygen partial pressure, the trait that enhances waterlogging tolerance in plants, was positively

correlated to SLA and negatively correlated to leaf thickness and cuticle thickness (while plasticity in these traits was not). Another extensive meta-analysis, comparing tens of species, suggested that the link between tolerance to oxygen stress and SLA response was significant but rather weak (Douma, Bardin, Bartholomeus, & van Bodegom, 2012).

While the examples above suggest some coordination for individual trait sets, when analysing tolerance towards waterlogging (presumably related to wetland adaptive traits) versus shade or drought (as related to LES/PES traits), a decoupling seems to prevail. A study of 806 shrubs/trees across continents suggested that correlations among shade, drought and waterlogging tolerance indices were significant but very weak (Hallik, Niinemets, & Wright, 2009; Niinemets & Valladares, 2006). This suggests that oxygen stress-related traits (waterlogging tolerance) might be decoupled from leaf economics traits (shade tolerance). Also, the fact that environmental drivers of the LES/PES traits are different from those driving wetland adaptive traits suggests that some orthogonality may occur among these sets of traits.

Given the partially contradictory evidence listed in our qualitative literature review and since none of the above studies specifically tested the relationships of different trait axes, we provide an exploratory quantitative analysis in the next section.

3 | EXPLORATION OF THE RELATIONSHIPS BETWEEN WETLAND ADAPTIVE TRAITS AND LES/PES TRAITS

To quantitatively explore the so far rather anecdotal and possibly contradictory relationships between wetland adaptive traits and LES/PES traits, we analysed a number of non-exhaustive published wetland ecophysiological studies and unpublished data sources, which presented trait measurements of both adaptive and LES/PES traits at the individual and species level under field or experimental conditions (see Supporting Information for data description details). In our analysis, we assume that individual wetland plants exert their adaptive strategies in response to environmental stress, independent of whether the exposure happened in the field or at experimental conditions. For our exploratory analysis on the relationships between adaptive traits and LES/PES traits, we focused on three pairs of relationships (root porosity vs. leaf N, ROL vs. leaf N, and iron tolerance vs. SLA), for which sufficient data were available for quantitative analysis. Root porosity and ROL are two very important ecophysiological adaptive traits at flooded conditions (Colmer, 2003b; Visser, Colmer, Blom, & Voeseinek, 2000; Voeseinek & Bailey-Serres, 2015), and reduced iron along with other reduced toxins is considered as the cause of the absence of non-wetland plants in wetland conditions (Snowden & Wheeler, 1993). Leaf N and SLA are leading traits driving the LES/PES axis (Diaz et al., 2016; Wright et al., 2004).

Previous studies have commonly observed a high degree of both interspecific and intraspecific variations in root porosity in wetland plants in response to oxygen stress (Lemoine et al., 2012; Mei, Yang,

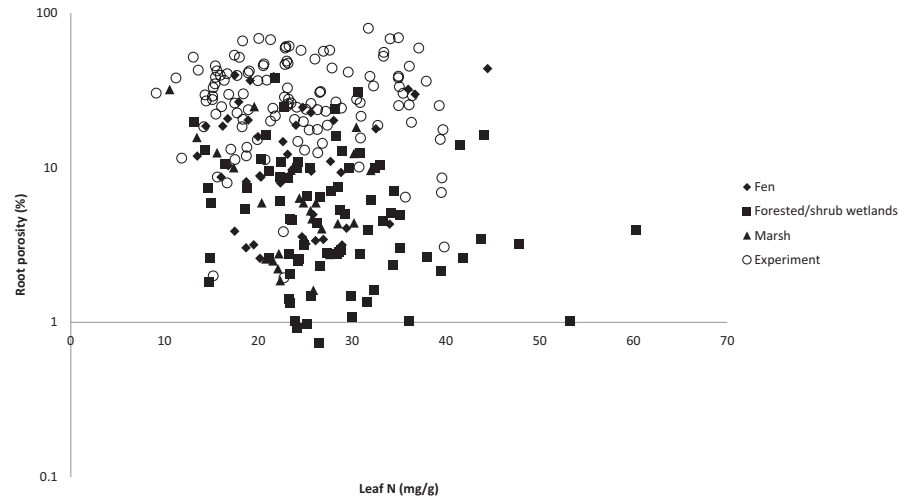
Tam, Wang, & Li, 2014), while leaf N varies according to soil fertility (following a gradient of acquisitive to conservative strategies) at the interspecific level (Maire et al., 2015; Ordoñez et al., 2009). To test the relationships between root porosity and leaf N, we collated data from three sources where both variables were measured on the same individuals (see Supporting Information Appendix S1 for further details): (a) glasshouse experiment in which six wetland plant species were measured in a 2×2 factorial design with soil oxygen demand (SOD) and partial submergence as the main factor (van Bodegom, Sorrell, Oosthoek, Bakker, & Aerts, 2008); (b) a field study in Ukraine, where root porosity and leaf N of 53 species from forested/shrub wetlands and marsh habitats were measured at field conditions (unpublished data, Supporting Information Figure S3a–c in Appendix S1); and (c) a field study in the Netherlands, where root porosity and leaf N of 22 species from fens were measured at field conditions (unpublished data, Supporting Information Figure S3a–c in Appendix S1).

A linear regression between leaf N and (log-transformed) root porosity (Figure 2) showed that, despite a significant correlation ($p < 0.01$), the very low R^2 (adjusted $r^2 = 0.030$; $n = 267$) indicates that only 3% of the variation can be explained by the model. At a high sample size—such as here—a significant relationship does not necessarily imply ecological relevance (Møller & Jennions, 2002; Yoccoz, 1991). The low effect size effectively represents a decoupling (Figure 2).

To test the relationships between ROL and leaf N, data were available from a glasshouse experiment, where five typical wet dune slack species were grown under all possible combinations of treatments with two (strongly differing) levels of light, fertility, reduced metal concentration and water regime gradients (van Bodegom et al., 2005). To be able to test this relationship, and because ROL data were heavily zero-inflated (92 out of 209 measurements showed no ROL), we grouped the ROL data into four classes in order to meet the normality assumption. The first class contained all 92 ROL observations, and the remaining 117 points were evenly divided into the other three classes in the ascending order (39 measurements for each bin). Subsequently, a linear model was run to test whether log-transformed leaf N varied as a function of ROL class. Despite a significant p value (which, again, we would consider induced by the large sample size), the overall lack of relationship ($r^2 = 0.053$) between log-transformed leaf N and ROL classes again suggested decoupling (Figure 3).

Results from these datasets suggest that: (a) potentially decoupled relationships between wetland adaptive traits and LES/PES traits may exist. Such decoupling indicates that the cost of, for example, root porosity formation might be relatively low for wetland plants and that a higher transportation capacity of oxygen to the rhizosphere (ROL) does not necessarily impede the nitrogen uptake capacity or the nitrogen utilization within plants, and (b) almost a full range of leaf N was covered (3.4 to 60.3 mg/g) compared to the leaf N range of terrestrial plants world-wide (2.48–68.98 mg/g) (Diaz et al., 2016). This full range of leaf N in wetland plants suggests that adaptation to wetland conditions is not necessarily costly (in agreement with Figure 1b). This is also supported by evolutionary

FIGURE 2 The relationships between root porosity and leaf N. The data are from measurements from a glasshouse experiment (van Bodegom et al., 2008) and field measurements of three habitats: fen, marsh and forested/shrub wetlands (P. M. van Bodegom, unpublished data, Supporting Information Figure S3a–c in Appendix S1)



evidence: aquatic species have evolved at least 200 times from terrestrial species (Cook, 1999).

Another type of adaptive traits relates to the tolerance, rather than avoidance or escape, of stressful conditions in wetlands. As a key stress tolerance characteristic of wetland plants, iron tolerance has been long considered as the cause for differential survival, growth and distribution among wetland plants (Snowden & Wheeler, 1993). Iron reduction along with manganese reduction takes place in the redox sequence after the depletion of nitrate, and produces phytotoxic ferrous iron. The physiological mechanisms behind iron tolerance are probably a combination of oxidation of the rhizosphere (partly contributed by ROL) and a true tolerance for Fe^{2+} . Due to a lack of quantitative traits expressing these true iron tolerance mechanisms, we used the iron tolerance index proposed by Snowden and Wheeler (1993) as a proxy trait. In that study, an iron tolerance experiment was set up for 44 British fen species seedlings, cultivated under in 10% Rorison solution containing reduced iron (as ferrous sulphate). The iron tolerance index was estimated based on the impact of iron on the relative growth rate (RGR) in comparison with the RGR in a control group (Snowden & Wheeler, 1993). To test how iron tolerance relates to LES/PES traits, we derived SLA of the corresponding species (with the exception of *Oryza sativa* which was not available) from the LEDA database (Kleyer et al., 2008). A linear regression between the iron tolerance index and SLA showed that the iron tolerance index decreased strongly and significantly with an increasing SLA ($r^2 = 0.237$, Figure 4).

This pattern may indicate a true trade-off between iron tolerance trait and LES/PES traits. We hypothesize that tolerance—in contrast to avoidance or escape traits—may be costly and hence induce coupling with LES traits. It will require further experimental work to test this hypothesis more fully with other traits and in other systems. Such experimental evaluation should consider other LES traits than SLA in relation to tolerance, given that SLA may also directly play a role in wetland adaptation (as discussed in Section 2).

The three exploratory investigations presented here suggest that both potentially coupled and decoupled relationships exist between wetland adaptive traits and LES/PES traits. The varied wetland adaptive traits may therefore not position along one trait axis,

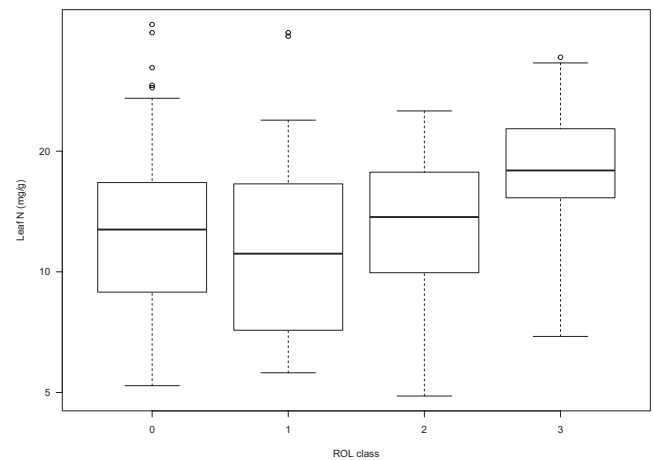


FIGURE 3 Box plot of leaf N across radial oxygen loss (ROL) class (adjusted $r^2 = 0.053$, $p < 0.01$, $n = 209$). Class 0: $\text{ROL} = 0 \mu\text{mol O}_2 \text{ h}^{-1} \text{ g root dry weight}^{-1}$, $n = 92$; class 1: $\text{ROL} = 2.5\text{--}21.5 \mu\text{mol O}_2 \text{ h}^{-1} \text{ g root dry weight}^{-1}$, $n = 39$; class 2: $\text{ROL} = 21.6\text{--}85 \mu\text{mol O}_2 \text{ h}^{-1} \text{ g root dry weight}^{-1}$, $n = 39$; class 3: $\text{ROL} = 90\text{--}1,212 \mu\text{mol O}_2 \text{ h}^{-1} \text{ g root dry weight}^{-1}$, $n = 39$. Data source: van Bodegom et al. (2005)

but some of them may be decoupled from one another. This implies that the selective forces in wetlands act in varied directions. The cost of developing a wetland adaptive trait may vary, depending on the trait and the conditions. The varied relationships between the two suites of traits suggest a variety of possible adaptive strategies to deal with specific combinations of wetland conditions, including both flooding stress and nutrient acquisition aspects.

4 | SCALING FROM WETLAND PLANT TRAITS TO ECOSYSTEM FUNCTIONING

Considering the importance of wetland ecosystems to humans, with regard to ecosystem services including water quantity and quality regulation and habitat provisioning for water birds and fish (Doherty

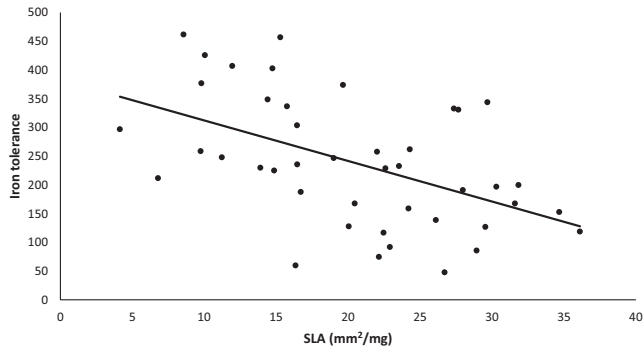


FIGURE 4 The relationship between specific leaf area (SLA) and iron tolerance (linear regression, adjusted $r^2 = 0.237$, $p < 0.001$, $n = 43$). SLA data were from the LEDA database (Kleyer et al., 2008), and iron tolerance data were estimated by Snowden and Wheeler (1993)

et al., 2014; Zedler, 2003), more and more attention is being paid to understanding wetland ecosystem functioning. Trait-based approaches have been applied to characterize plant strategies and their effects on ecosystem functioning of wetlands (Moor et al., 2017), but such studies have mainly focused on LES/PES traits (Douma et al., 2012). However, given the unique adaptive traits in wetland ecosystems, these need to be additionally considered to fully understand trait-based impacts on wetland ecosystem functioning. For instance, two important biogeochemical processes in wetlands, denitrification and methane production, depend on soil organic matter content—which are strongly influenced by community mean leaf nitrogen and carbon concentrations (LES/PES traits) (Koschorreck & Darwich, 2003)—and suitable aerobic/anaerobic conditions, which relate to ROL and root porosity (adaptive traits) (Allred & Baines, 2016; Engelhardt, 2006; Sutton-Grier, Wright, & Richardson, 2013).

Knowledge of the combined effects of adaptive traits and LES/PES traits can thus improve our understanding of denitrification and methane production, which is important for the sustainable management of wetlands, including the reduction of greenhouse gas emissions by wetlands and the relief of eutrophication in wetlands.

In addition to affecting the functioning of wetlands, wetland adaptive traits may also affect the community structure of wetlands in a complicated way. ROL relates to oxygen leaking from roots into the soil, which results in microaerophilic conditions in the rhizosphere (van Bodegom & Scholten, 2001). This allows detoxification of several potentially toxic compounds such as S^{2-} and Fe^{2+} . The microaerophilic conditions induced by ROL do not only favour growth of the plant species that have ROL, but also facilitate the growth of less-adapted species that would not survive under purely anoxic soil conditions (Schat, 1984). As a consequence, the facilitation of these less-adapted species leads to a competition with the adapted species and a higher turnover of species than would have occurred otherwise (Grootjans, Ernst, & Stuyfzand, 1998).

Radial oxygen loss also contributes to community composition in a more direct way, through its coupling of the nitrification and

denitrification processes. Compared to cases in which ROL is absent, the increased availability of soil oxygen in communities with ROL induces nitrification. The produced nitrate diffuses into the anoxic bulk soil and is denitrified, and hence leads to increased nitrogen losses and decreased nutrient availability in wetland ecosystems (Adema, Van de Koppel, Meijer, & Grootjans, 2005; Reddy, Patrick, & Lindau, 1989). Low nutrient availability makes it harder for competitors to invade, as many grow less effectively in such an environment. As a consequence, the community of stress-tolerating plant species that grow less quickly at high nutrient levels may remain more stable (Adema & Grootjans, 2003).

This feedback loop between ROL and denitrification is further complicated because both ROL (through oxygen supply for nitrification) and LES/PES traits by a combination of direct and indirect relations determine nitrate availability. If ROL is orthogonal to leaf N (as suggested by the exploratory analyses described above), these two influences on nitrate availability and hence denitrification may occur independently from each other. However, if there is a trade-off between ROL and leaf N, then nitrate sources can be limited by low ROL leading to a natural reduction of denitrification. In that case, a strong nitrification/denitrification coupling is not expected to occur. This example again demonstrates the importance of understanding the relationships between wetland adaptive traits and LES/PES traits.

Methane emission is another example that shows how wetland adaptive traits and LES/PES traits together affect ecosystem functioning. Methane production only takes place after most other alternative electron acceptors have been depleted. Both production and emission of methane are affected by wetland plants in many aspects. First of all, organic compounds released by root exudation can be used as electron donors for methane production (Aulakh, Wassmann, Bueno, & Rennenberg, 2001). Second, oxygen released from the roots may be used by bacteria to oxidize methane to CO_2 , decreasing methane emissions (van Bodegom, Goudriaan, & Leffelaar, 2001). Third, the aerenchyma channels of wetland plant species act as chimneys that effectively transport methane from the soil to the atmosphere. This plant-mediated transport pathway is much more effective than diffusion through the soil alone (van Bodegom, Groot, van den Hout, Leffelaar, & Goudriaan, 2001, Figure 5) and decreases the probability of methane oxidation. The combination of adaptive traits and local conditions (such as temperature, water level, soil texture) determines whether the net effect of wetland plants is an amplification or decrease of methane emissions.

To further advance our quantitative understanding of strategies and functioning (including denitrification and methane emission) in wetlands, we identified a number of critical research topics that would benefit from an inclusive approach. First, we need to target specific pairs of wetland adaptive traits and LES/PES traits and study them quantitatively to better understand the nature and patterns of this relationship. Specifically, such analysis may test the hypothesis that tolerance traits may be coupled while avoidance and escape traits are not. Second, the drivers determining the selection of these different trait sets will have to be analysed. Third, based on an understanding of which traits do and which do not couple to LES traits and under which conditions, combined with knowledge on how

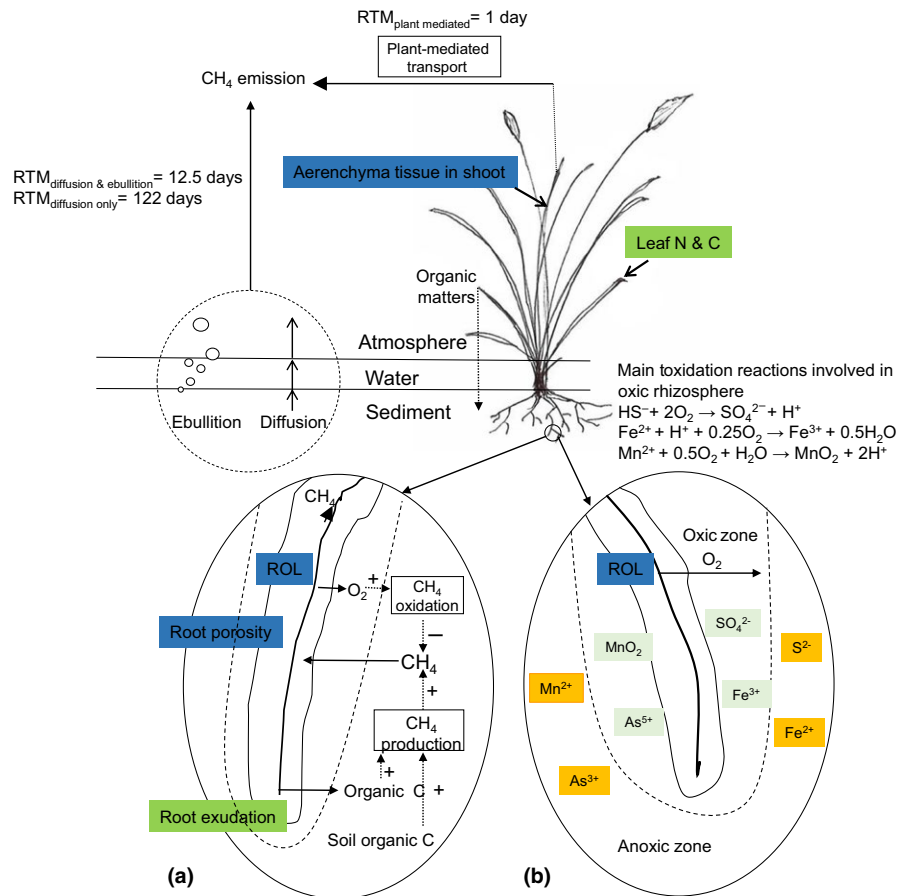


FIGURE 5 Schematic presentation of the wetland adaptive traits (in blue boxes) and leaf economics spectrum (LES)/plant economics spectrum (PES) traits (in green boxes) impact on (a) the gas transportation through wetland plants and organic compound release and (b) oxidation reactions in oxic rhizosphere (with oxidized elements in purple boxes and reduced elements in orange boxes). The residence time of methane (RTM) in soil is based on data discussed in Bodegom, Wassmann, et al. (2001)

the interplay of adaptive and LES traits affects important wetland ecosystem functions, the variation in these ecosystem functions at the global scale can be quantified and understood. Such insights will help recognize the importance of wetland ecology in times of global change.

5 | CONCLUSIONS

By bridging the fields of study of wetland adaptive traits and LES/PES traits and their relationships, we can unravel wetland plant strategies and obtain a broader picture of wetland ecology. Our work provides a first exploration of such relationships through a qualitative literature review and a quantitative assessment between examples of the two suites of traits; this can be further explored in future wetland ecology research. Our analyses suggest both coupled and decoupled patterns do occur between wetland adaptive traits and LES/PES traits, and provide a first glimpse at the complex character of adaptation in wetland ecosystems. Further unravelling the relationships between the two suites of traits will be critical to understanding wetland ecosystem functioning, especially for those processes to which multiple traits contribute, such as denitrification and methane emissions, and that are globally important processes of greenhouse gas emissions. To fully reveal the patterns between adaptive traits and

LES/PES traits, we are in need of global compilation and analysis of trait datasets.

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AUTHORS' CONTRIBUTIONS

P.M.v.B. conceived the study; Y.P., E.C. and P.M.v.B. developed the ideas; P.M.v.B. and Y.P. collected the data; Y.P. wrote the first draft and conducted the analyses. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are deposited in the Dryad Repository: <http://doi.org/10.5061/dryad.4v1s6b5> (Pan, Cieraad, & Van Bodegom, 2019).

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